

GENETICS AND BREEDING

Holstein Conversion Equations Based on Population Variances and a Full-Brother Model

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ABSTRACT

A full-brother method was used to develop conversion equations that predict US Holstein PTA for milk, fat, and protein yields from French EBV. Regression coefficients were ratios of genetic standard deviations of sires for the two populations adjusted for the genetic correlation between countries. Based on data from full brothers, the regression coefficients were used to determine the base differences of countries (intercepts), scaled to the variation in the importing country. Full-brother equations also were developed to convert evaluations from Canada and The Netherlands to a US equivalent so that the full-brother method could be compared with traditional methods. Genetic correlation with the US was assumed to be .9 for French data and 1.0 for data from Canada and The Netherlands. Standard deviations for the populations were computed from nearly 5900 US bulls and about 2000 bulls from each of the other countries. The US had 178 full-brother families in common with France, 123 in common with Canada, and 46 in common with The Netherlands. For conversion of Canadian evaluations to a US equivalent, regression coefficients from the full-brother method were 20% lower than from the Goddard method and 25% lower than from the Wilmink method. (Key words: conversion, genetic evaluation, population variance, family)

Abbreviation key: BCA = breed class average, DYD = daughter yield deviation, INTER-BULL = International Bull Evaluation Service, REL = reliability, r_g = genetic correlation.

INTRODUCTION

Genetic evaluations of dairy bulls are expressed in different ways by different countries. Just as for language and currency, expressions of genetic merit require translation or conversion to be understood across countries. Bull evaluations may be in terms of EBV or ETA, which is half of EBV. Further, units may be kilograms, pounds, or various relative or percentage expressions. Beyond these obvious scaling differences, critical differences exist in evaluation methodology that require consideration. Combinations of factors, such as base age for standardization of lactation records, heritability used, completeness of model, and adjustment for heterogeneous variance, affect scaling.

After evaluations are placed on the same multiplicative scale, they must be placed on the same additive scale for alignment. Basically, this alignment is an estimation of what an evaluation for a bull with an evaluation of 0 in one country would be in another country. Differences among countries in the expression of genetic merit for bulls with an evaluation of 0 reflect both differences in genetic levels of populations and differences in base definitions.

Conversion equations consist of intercepts (a) and scaling factors or regression coefficients (b): converted evaluation for importing country = $a + b(\text{reported evaluation in exporting country})$. The Goddard (4) and Wilmink (14) methods have been approved by the International Bull Evaluation Service (INTER-BULL) (5) for use in development of conversion equations. These methods require evaluations of a common group of bulls to determine a and b. Schaeffer (11) proposed a linear model for combination of national evaluations to produce international evaluations. With this method, b were determined from ratios of population standard deviations, and a was a by-product of the combined evaluation. To remove effects of preferential treatment that

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appeared to be present for daughters in countries of later use, Banos (2) suggested a modification of Schaeffer's method that would eliminate evaluations in countries subsequent to progeny test in the initial country. The likelihood of preferential treatment of daughters from imported semen also had been reported by Powell et al. (9). A crucial point of the linear model approach is the choice of data included (2). Schaeffer (12) proposed a modification to his earlier approach that would account for genetic correlations of <1.0 by treatment of evaluations for bulls in different countries as separate, correlated traits.

In France, foreign bulls (other than those few that are simultaneously sampled with local bulls) do not have their French evaluations released. The reasons for not releasing evaluations for these bulls are the likelihood of preferential treatment of their daughters and the use of their semen in only a few special herds disconnected from the bulk of the French data (J.-C. Mocquot, 1993, personal communication). Because the Goddard (4) and Wilmink (14) methods required a common group of bulls with evaluations in both countries, official equations to convert French evaluations to a US equivalent had not been developed. The problems with conversion equations generated against the gene flow have been shown by Banos (3) in a simulation study and by Powell et al. (9) with empirical data. Thus, although the availability of French evaluations for US bulls would have allowed calculation of conversion equations, results would not have been ideal. The existence of official equations to convert French evaluations to a US equivalent was primarily of academic interest until late 1993 when semen from 5 Holstein bulls was imported into the US from France. Four of the bulls were from North American breeding, and the remaining bull was 87.5% North American.

French researchers have suggested an alternative approach to obtain conversion equations for Holsteins (7). Although the French conversion procedure has been labeled the full-brother or full-sib method, the b are calculated from population data (rather than data only from full brothers) in the same way as suggested by Banos (2) for the linear model. Base differences were from a comparison of full brothers in the US and in France. Mattalia and

Bonaiti (7) reported 163 families with at least one full brother in each country. An advantage of this full-brother method over the approaches of Schaeffer (11, 12) is that mates of specific maternal grandsires do not have to be assumed to have equal merit, regardless of country (7).

Objectives of this study were to develop equations to convert French evaluations to a US equivalent based on population variances and a full-brother model and to compare equations from that approach to results from other countries where Goddard (4) and Wilmink (14) equations can be obtained.

MATERIALS AND METHODS

Genetic evaluations for Holstein bulls were from January 1994 for the US and Canada, March 1994 for France, and April 1994 for The Netherlands. Bulls from France were required to have both parents from the US, but bulls from The Netherlands only had to have US sires. Parents for US and Canadian bulls could be from either country, but the bulls were required to have had their first evaluation in that country as part of an AI program. Bulls from all countries had birth years of ≥ 1981 and ≥ 35 daughters in ≥ 20 herds. The US bulls were from eight major AI organizations, had semen distributed at <40 mo of age, and had a sampling code other than O assigned by the National Association of Animal Breeders (10).

Regression Coefficients

The regression coefficients (b) were determined as a function of ratios of genetic standard deviations of sires for each population. As suggested by Banos (2), the standard deviations for each country and trait were the geometric means (square root of the product) of the standard deviations of ETA and daughter yield deviations (DYD) (13). The DYD are a form of ETA, not EBV. Because evaluations from France and The Netherlands were in EBV, the standard deviations for those evaluations were halved prior to computation of the geometric mean, because initial application of b was to scale DYD for determination of a . The standard deviations were computed by birth year of bull by fitting a model in which DYD and ETA were explained by birth year. Standard deviations for the residuals were then computed, and, finally, the geometric mean of

those standard deviations were calculated by trait. In general, standard deviation of ETA increases toward the genetic standard deviation of sires as reliability (REL) increases, but standard deviation of DYD decreases toward the genetic standard deviation of sires.

The regression coefficients were calculated as

$$b = (SD_i/SD_e)r_g$$

where SD is estimated genetic standard deviation of sires, i indicates the importing country, e indicates the exporting country, and r_g is the genetic correlation between the genetic merits in the two countries. For the US and France, r_g of .90 and 1.0 were analyzed, but only an r_g of 1.0 was assumed between the US and either Canada or The Netherlands. These b were used to determine a and were halved for use in equations to convert foreign evaluations expressed as EBV to a US equivalent.

Intercepts

In general, bulls used for determination of intercepts (a) were a subset of the bulls used for calculation of b . However, bulls were accepted from other than the eight major US AI organizations. The full brothers for estimation of an intercept (a) were chosen through a three-step procedure: 1) bulls that met birth year, REL, and parent origin requirements were selected from the non-US country; 2) US bulls with the same parents (i.e., full brothers) were identified; and 3) only families identified in both the US and the other country were retained. For the US and France, 178 sets of parents (families) had 253 qualifying US sons and 291 French sons. The 123 full-brother families in the US and Canada had 175 US bulls and 136 Canadian bulls, and the 46 full-brother families in the US and The Netherlands had 64 US bulls and 73 bulls from The Netherlands.

Country base differences (intercepts) were determined from the model

$$y_{ijk} = c_i + f_j + e_{ijk}$$

where y_{ijk} = DYD for member k of full-brother family j in country i , c_i = fixed effect of country i where i is either the US or France, f_j

= fixed effect of full-brother family j , and e_{ijk} = random residual. The exporting country's DYD were placed on the scale of the importing country by multiplication with the appropriate b . Intercepts (a) were computed as the solutions for the importing country minus the solutions for the exporting country.

Comparison of Conversion Methods

For Canada and The Netherlands, conversion equations derived from the full-brother approach were compared with those from the Goddard (4) and Wilmink methods (14), based on 1994 requirements for official equations. Data followed the general guidelines of INTERBULL (4), except that the minimum REL for both countries was >75%. The 158 bulls used to develop official equations to convert Canadian evaluations to a US equivalent were first sampled in Canada and had birth years of ≥ 1977 , daughters in ≥ 20 herds for each national evaluation, Canadian REL of $\geq 90\%$, and US REL of $\geq 75\%$. The 103 bulls used to develop official equations to convert evaluations from The Netherlands to a US equivalent had birth years of ≥ 1981 , daughters in ≥ 20 herds, and REL of $\geq 85\%$ in both countries. Although this conversion was against the gene flow, no other data were available for use as a reference.

RESULTS

Nearly 5900 US bulls and about 2000 from each of the other countries contributed to calculation of estimates of genetic standard deviations of sires (Table 1). These estimates were essentially the same for US bulls and 2 to 4% smaller for French bulls than those reported in the original French study (7). Data for the two studies were somewhat different in that the national evaluations included in this study were 1 yr more current for both countries. The standard deviations for France were similar to those reported by Miglior and Lohuis (8), but lower for milk and protein and higher for fat than those in an INTERBULL study (6). Standard deviations for The Netherlands were lower for milk, higher for fat, and nearly the same for protein compared with those reported in the INTERBULL study (6). Standard deviations for Canada were 3 to 4% larger than those found by Miglior and Lohuis (8). The

TABLE 1. Estimated genetic standard deviations of Holstein sires expressed as transmitting abilities for yield traits and numbers of bulls.

Country	Bulls (no.)	Sire genetic SD ¹		
		Milk	Fat	Protein
US	5885	285	10.17	7.90
France	1885	303	11.95	8.38
Canada	2119	7.156	7.112	6.412
The Netherlands	1999	243	8.74	6.41

¹Expressed in kilograms for the US, France, and The Netherlands and in breed class average points for Canada.

maximum difference found between the standard deviations in Table 1 and those reported in previous studies (6, 7, 8) was 4%.

Regression coefficients (b) based on the genetic standard deviations of sires are in Table 2. These b are for conversion from ETA in one country to ETA in a second country. Regardless of assumed r_g , the b for France to US conversion were larger than those reported by Mattalia and Bonaiti (7) because of the relative difference between the estimates of genetic standard deviations of sires from the two studies. A brief study of the b that would have resulted from only full-brother data indicated that these b were higher for all traits for Canada and France and higher for fat but lower for milk and protein for The Netherlands than were b based on population data (Table 2). The b from full brothers were based on much fewer data, and sampling is the only explanation proposed for the differences between population estimates and the full-brother subsets. The

b in Table 2 were used to scale the DYD from the non-US country to a US basis for use in the full-brother model, which produced base differences among countries.

Because DYD are expressed in terms of transmitting ability, as is PTA, the country solutions provided intercepts (a) for use in conversion equations (Table 3). Standard errors for the base differences showed that estimates were variable. Standard errors reflect the numbers of full-brother families and bulls included in the analyses. France had the most data and lowest standard errors, and The Netherlands had the least data and highest standard errors.

Table 4 presents the a and b from the full-brother, Goddard (4), and Wilmink (14) methods that would be used in conversion equations. The a for the full-brother method are from Table 3, and the b for the full-brother method are half the regression coefficients for Table 2, except those for Canada. Halving of b was necessary for conversion equations for

TABLE 2. Regression coefficients¹ for converting French, Canadian, and The Netherlands Holstein evaluations expressed as transmitting abilities for yield traits to US equivalents.

Trait	France		Canada ²	The Netherlands ²
	r _g = 1.0	r _g = .9		
			(kg/BCA ³ point)	
Milk	.941	.847	39.870	1.173
Fat	.851	.766	1.431	1.164
Protein	.943	.848	1.232	1.232

¹Calculated as $(SD_i/SD_e)r_g$, where SD is genetic standard deviation of sires in importing country i or exporting country e and r_g is genetic correlation.

²Assumed r_g of 1.0.

³Breed class average.

TABLE 3. Intercepts (a) and their standard errors for converting French, Canadian, and The Netherlands Holstein evaluations for yield traits to US equivalents.

Trait	France				Canada ¹		The Netherlands ¹	
	$r_g = 1.0$		$r_g = .90$					
	a	SE	a	SE	a	SE	a	SE
	(kg)							
Milk	257	23	279	22	206	30	-45	47
Fat	14.9	.8	15.4	.8	9.7	1.0	6.0	1.6
Protein	8.2	.7	8.8	.6	3.5	.8	.1	1.3

¹Assumed genetic correlation (r_g) of 1.0.

France and The Netherlands because their genetic evaluations are expressed as EBV rather than as ETA, as in Canada and the US. The Goddard a and b were from the official conversion equations computed by USDA in spring 1994. The Wilmink a and b were computed from the same data as for the Goddard equations. Standard errors for b were 3% of b for Canada and 6 to 7% of b for The Netherlands for Goddard (4) and Wilmink (14) equations.

For Canada, the a and b that were derived with the full-brother method were markedly higher and lower, respectively, than those obtained by the traditional methods. The b from the full-brother method were about 20% lower than those from the Goddard (4) method and about 25% lower than those from the Wilmink (14) method. Procedures or subsets of data that result in higher b generally produce lower a and vice versa (as occurred for Canada). Predictions of US PTA from the full-brother method would be lower than predictions from traditional methods for Canadian bulls with the highest evaluations and higher for bulls of low to moderate merit. Factors used in Canada to transform Holstein breed class averages (BCA) to kilograms are 53 kg/BCA point for milk, 1.96 kg/BCA point for fat, and 1.68 kg/BCA point for protein (1). Average evaluations for active AI Holstein bulls in Canada are about 12 to 14 BCA points (1). The equivalency point for the full brother and Goddard (4) methods was 10.76 BCA points for milk, 15.52 BCA points for fat, and 6.00 BCA points for protein. For Canadian evaluations with BCA lower than the equivalency point, predictions of US PTA based on the full-

brother method would be higher than would predictions based on official conversion equations; for Canadian evaluations with higher BCA, US PTA predicted from the full-brother method would be lower than official predictions.

For The Netherlands, b for milk and protein were lower from the full-brother method than from the Goddard (4) and Wilmink (14) methods, but higher for fat. As for Canada, higher a were associated with lower b and vice versa. Because of the limited number of families, the results for an intercept (a) were not too unusual, but b from the full-brother method differed from official b by about 10%.

DISCUSSION

The full-brother method allowed for computation of conversion equations to estimate US PTA from French Holstein EBV. The resulting equations were supported by French research (S. Mattalia, 1994, personal communication). Conversion equations between France and the US would not be reciprocal because of the assumed r_g of .9. The appropriateness of an r_g of .9 may be questioned on the basis of high r_g estimates by Powell et al. (9) and even higher estimates by Schaeffer (12). Conversely, rankings of the few bulls simultaneously sampled in the US and France were not as similar as expected, which supports an $r_g < 1$.

The more traditional Goddard (4) and Wilmink (14) methods use evaluations in two countries for the same bulls to develop conversion equations; the full-brother method uses data separated by one more genetic segregation. Thus, for a given degree of accuracy for

TABLE 4. Intercepts (a) and regression coefficients (b) from the full-brother (FB), Goddard (G), and Wilmink (W) methods to develop equations for converting French, Canadian, and The Netherlands Holstein evaluations for yield traits to US equivalents.¹

Trait	France ²						Canada ³						The Netherlands ²					
	$r_g = 1.0$			$r_g = .9$			a			b			a			b		
	a	b		a	b		FB	G	W	FB	G	W	FB	G	W	FB	G	W
	(kg)		(kg)	(kg)		(kg)					(kg/BCA ⁴ point)		(kg)					
Milk	257	.470	279	.423		206	78	62	39.9	51.8	55.2	55.2	45	-123	-141	.532	.585	.599
Fat	14.9	.426	15.4	.383		9.7	5.2	4.7	1.43	1.72	1.84	1.84	.60	9.5	9.1	.528	.474	.487
Protein	6.2	.471	8.8	.424		3.5	1.7	1.8	1.23	1.53	1.65	1.65	.1	-1.0	-.5	.559	.594	.597

¹French and The Netherlands evaluations are EBV; Canadian and US evaluations are ETA.²Full-brother method only; data not available for use of Goddard (4) and Wilmink (14) methods.³Assumed genetic correlation (r_g) of 1.0 for the full-brother method.⁴Breed class average.

a, the number of families for the full-brother method is greater than the number of bulls for the other methods. Numbers of families were adequate for US and French data, intermediate for US and Canadian data, and limited for US and The Netherlands data.

The b from full brothers were based on large numbers of bulls and should be both accurate and stable. The large differences in b between full-brother and official equations for Canada to US conversions raise serious questions. Are b that are currently used inflated, or is the procedure that uses population data to estimate b faulty? The latter is of greater concern because this procedure is essentially the same as that intended by the INTERBULL Centre for use in combination of bull evaluations across countries. Other methods for estimation of sire genetic variances may need to be employed, or further study may be required to validate theoretical b in conversion equations.

CONCLUSIONS

The full-brother method provided reasonable conversion equations that should be free of bias because of preferential treatment of daughters from expensive semen of popular bulls. Having a sufficient number of full brothers is a drawback for most pairs of countries, but large numbers were available for the US and Canada and, especially, the US and France. Estimates of b should be accurate because they were based on data from thousands of bulls. However, the ratio of genetic standard deviations of sires does not account for r_g of <1 as is automatically considered by the Goddard (4) and Wilmink (14) methods.

Although no weakness in the full-brother method is apparent for conversion of Canadian BCA to US PTA, the large differences in the equations (particularly for b), compared with those from traditional methods, were disconcerting. Further research may uncover an improved method or reconcile the current conflicts.

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